

Movement and Recolonization of Potomac Sculpin in a Virginia Stream

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Abstract.—Movement patterns of benthic fishes have not been widely studied, but an understanding of those movement patterns may be necessary in assessing the full effects of habitat fragmentation and the need to restore connectivity in fragmented watersheds. We evaluated nonspawning movement of 3,353 marked Potomac sculpin *Cottus girardi* over a 1-year period on a 3.14-km segment of a third-order stream. In addition, we conducted a fish removal experiment at the pool–riffle sequence scale (90 m) to evaluate the effects of fish density on movement and recolonization rates. The majority of recaptured Potomac sculpin stayed within 30 m of their original capture location throughout the study (81% at 30 d; 64% at 75 d; 53% at 363 d). Upstream (US) movement was greater than downstream (DS) movement at 30 d (US 17%; DS 3%), 75 d (US 30%, DS 6%) and 363 d (US 32%, DS 15%). After 75 d, 10% of the fish that moved upstream moved more than 250 m (21% after 363 d). The maximum distance moved was 1,711 m in 75 d. There were no significant differences in mean total length between recaptured Potomac sculpin that either moved or did not move or between upstream and downstream movers. The presence or absence of fishes in adjacent 30-m habitat sections influenced upstream, but not downstream, movement of Potomac sculpin. After 30 d, Potomac sculpin population densities and size structure were similar between fish removal and reference sections. We found our results to be similar to those of other studies, which found that, on average, freshwater sculpin are sedentary. However, we identified great dispersal capabilities (>250 m) for a small percentage of Potomac sculpin. The long dispersal distances suggest that this typically sedentary species may need greater habitat connectivity than previously assumed.

Information on movement is necessary for assessing the full effects of fragmentation and a species' population needs when restoring connectivity in fragmented watersheds. The short-term and long-term movement patterns of many benthic fishes are unknown, but, in general, home ranges appear to be small. While there has been considerable research on fish movements in general (see reviews by Gowan et al. 1994; Matthews 1998; Rodriguez 2002), most work has focused on salmonids and other sport fish.

Previous research has indicated that most freshwater sculpins (Cottidae) do not move frequently or far (see Table 1 for a detailed summary), but no current information has been published on the movement patterns of Potomac sculpin *Cottus girardi*. Matheson (1979) and Jenkins and Burkhead (1993) do, however, summarize the general ecology and taxonomy of the Potomac sculpin.

Bailey (1952) concluded that mottled sculpin *Cottus bairdii* were relatively sedentary, with typical yearly movements of 50 m. McCleave (1964) estimated the home range of mottled sculpin to be less than 50 m. In two Montana streams, mottled sculpin movement

during nonspawning times (June and July) was found to be short (mean = 1.2 m) and haphazard (no preference for upstream or downstream movement) (Brown and Downhower 1982). Brown and Downhower (1982) concluded that mottled sculpins are capable of relatively great dispersal movements but are actually quite sedentary. A study by Hill and Grossman (1987) found mottled sculpin to have an estimated home range of 12.9 m. Greenberg and Holtzman (1987) found the maximum home range of the banded sculpin *Cottus caroliniae* to be 47 m². Morgan and Ringler (1992) found approximately 80% of marked slimy sculpin *Cottus cognatus* within the original 50-m release site. Less than 20% of the slimy sculpin migrated, and 80% of those moved less than 25 m. Natsumeda (1999) found that the mean movements of the male and female Japanese fluvial sculpin *Cottus pollux* was less than 20 m. Petty and Grossman (2004) found that most individual mottled sculpin moved less than 3 m. The longest movement of slimy sculpin and a second, undescribed sculpin species documented by Schmetterling and Adams (2004) was 209 m. Greater distances may have been observed if traps had not obstructed movement. Some stream fishes can be highly mobile, and recolonization by some fish assemblages can occur on the scale of days or weeks (Peterson and Bayley 1993; Lonzarich et al. 1998,

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Received June 13, 2007; accepted June 6, 2008

Published online February 23, 2009

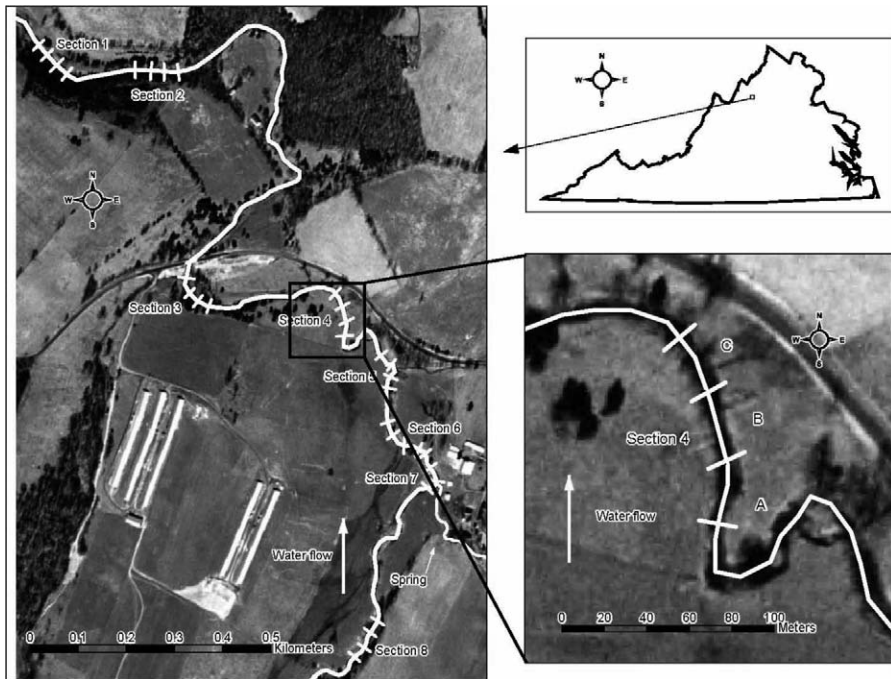


FIGURE 1.—Smith Creek study area with (1) location of the eight 90-m sections and 24 habitat reach subsections where fish were marked (Subsections [A] upstream; [B] middle; and [C] downstream) and (2) the entire 3.14-km sampling area.

2000). However few recolonization studies have included freshwater sculpins. If freshwater sculpins are generally sedentary and have small home ranges, how do they colonize available habitat after stochastic or anthropogenic events, or after restoration activities such as dam or culvert remediation?

We describe the short-term and long-term movement patterns and short-term recolonization rates of a population of Potomac sculpin. The specific objectives of this study were (1) to evaluate short-term (30 and 75 d) and long-term (367 d) movement patterns of Potomac sculpin at two scales (eight 90-m and one 3.17-km sampling areas) in an unfragmented stream, and (2) to evaluate short-term recolonization rates after 30 d in 30-m sampling sections with and without fishes.

Methods

Study area.—Smith Creek is a third-order stream within the 5,539-ha Smith Creek subwatershed in western Virginia (Hydologic Unit Code 510172). Smith Creek is a pool-riffle stream with an average gradient of 1.74%, and an average wetted width of 7.1 m. Most of the overall subwatershed, as well as the riparian areas (100 m each side of stream), are classified as forested (61% and 56%, respectively) or agricultural (38% and 42%, respectively) (USGS 2004;

Thieling 2006). However, the 3.14-km study reach has few riparian trees (113 trees greater than 10-cm diameter breast height) and is predominately heavily grazed pasture (Figure 1).

We conducted two distinct sampling regimes to evaluate both short-term (30–75 d) and long-term (up to 367 d) movement and recolonization patterns for Potomac sculpin. The first sampling regime was at a 90-m scale (pool-riffle sequence) and the other was along a 3.14-km section of stream.

90-m sampling.—We selected eight representative 90-m sampling areas on Smith Creek. Each 90-m sample was divided into three 30-m subsections (upstream, A; middle, B; downstream, C) (Figure 1). We conducted three- to four-pass depletion population estimates using electrofishing (Zippin 1956) on each of the 24 subsections during June 2005 (9 June 2005 to 27 June 2005), July 2005 (21 July 2005 to 2 August 2005), and July 2006 (24 July 2006 to 27 July 2006). Upstream and downstream block nets were used during all depletion sampling.

During the June 2005 sampling, all Potomac sculpin captured in subsections A (upstream) and C (downstream) were measured to the nearest millimeter in total length (TL) and given a visible implant elastomer (VIE) mark unique to each of the subsections (Roberts and Angermeier 2004; Figure 1). All fish were then

TABLE 1.—Summary of findings from selected references on cogenetic freshwater sculpin. Abbreviations are as follows: N = collected by hand, net, or trap; E = collected by electrofishing; NA = not applicable for this reference; US = upstream; DS = downstream.

Species	Location: state or country	Mean movement or home range (HR)	Collection method	Size differences between mobile and nonmobile	Maximum movement (maximum detection)
Mottled sculpin	Montana	50 m	N, E	NA	156 m (766 m)
	Montana	<50 m	E	NA	180 m (242 m)
	Montana	1.2 m	N	None	14.3 m (1,600 m)
	North Carolina	12.9 m (HR)	N	NA	55 m (100 m)
Banded sculpin	Tennessee	<6 m	N	NA	6 m (25 m)
Slimy sculpin	New York	50 m (80% within)	E	NA	NA
Fluvial sculpin	Japan	>20 m	N	NA	290 m (400 m)
Mottled sculpin	North Carolina	<1–8 m	N	Yes	165 m (>250 m)
Slimy sculpin	Montana	18 m (Median)	N	None	209 m

released in the middle of the subsection of capture. Marked fish bracketed each of the B (middle) subsections ($n = 8$), which were a priori randomly assigned to either a reference or a removal treatment group.

In the removal subsections all fish were measured to the nearest millimeter TL and then removed from the subsection. In reference subsections all fish were measured to the nearest millimeter TL and then released unmarked in the middle of the subsection of capture. During the July 2005 and July 2006 samplings, we only conducted population estimates and looked for recaptures. No additional fish were marked.

Potomac sculpin recaptured in the same 30-m subsection in which they had been marked were classified as having no movement (NM). Fish that moved beyond their original marking subsection were classified by the direction of movement as either upstream (US) or downstream (DS).

During repeated sampling of the 90-m reaches, we could detect movement (US or DS) by any marked fish that moved into and stayed in the B (middle) subsection of the same 90-m sample or moved into any one of the other 90-m sample areas. We could not detect marked fish that moved and stayed between any of the eight 90-m sampling units (Figure 1).

The potential upstream movement that we could detect during resampling of the 90-m reaches varied by reach from 30 to 2,762 m, and averaged 1,205 m ($SD = 915$ m). Potential downstream movement varied by reach from 30 m to 2,762 m and averaged 1,556 m ($SD = 916$ m).

3.14-km sampling.—In August 2005 (about 75 d after marking fish in the 90-m sampling areas) and August 2006 (average 367 d after marking), we conducted a one-pass electrofishing sample throughout the 3.14-km study area. All fish captured were recorded by species and checked for VIE tags.

The maximum distance of potential upstream movement that we could detect during the 3.14-km sampling varied by which 90-m stream section a fish was marked in but averaged 1,575 m ($SD = 917$; range = 386–3,140 m). Downstream movement varied by study section from 30 to 2,792 m and averaged 1,596 m ($SD = 918$ m).

Stream temperature and flow.—We placed thermographs (HOBO Water Temp Pro; Onset Computer Corporation, Bourne, Massachusetts) that recorded air and water temperatures at the midpoint of all eight 90-m sampling sections. An additional 19 thermographs recorded water temperature throughout the 3.14-km study area. Air and water temperatures were recorded throughout the entire study in 30-min increments. Thermographs were calibrated and tested for drift at the end of the study. A permanent stream gauge and hydrograph (HOBO water level logger; Onset Computer Corporation) was established in the midpoint of the study area. Flows were calculated for 30-min increments during the study period.

Statistical analysis.—We evaluated our short-term and long-term movement pattern objectives by comparing differences among the three movement groups (NM, US, and DS) at various time intervals (30, 75, and 367 d) using a chi-square test. Equal distributions were assumed. The shift in the proportions of the movement groups among time periods was evaluated with a Pearson's chi-square. We used an analysis of variance (ANOVA) or paired *t*-tests to compare differences in total length of Potomac sculpin from the movement groups. We tested skewness (Zar 1996) and kurtosis (Anscombe and Glynn 1983) of the patterns and distributions of the three movement groups.

In evaluating our short-term recolonization objectives, we used *t*-tests or Mann-Whitney *U*-tests (depending on normality) to test for differences in density, mean lengths, or the percentages of recaptures

TABLE 1.—Extended.

Species	Number marked	Percent recaptured once	Length of study (d)	Movement preference (None, US, DS)	Reference
Mottled sculpin	75	28	205	NA	Bailey (1952)
	212	23.9	216	US	McCleave (1964)
	188	39	22	None	Brown and Downhower (1982)
	180	28	458	NA	Hill and Grossman (1987)
Banded sculpin	34	33	90	NA	Greenberg and Holtzman (1987)
Slimy sculpin	NA	NA	98	NA	Morgan and Ringler (1992)
Fluvial sculpin	1,418	21.9	322	None	Natsumeda (1999)
Mottled sculpin	604	>75	1,095	None	Petty and Grossman (2004)
Slimy sculpin	172	33.7	22	DS	Schmetterling and Adams (2004)

between removal and reference subsections. We also reported mean values with Mann–Whitney *U*-test results. A Pearson's chi-square was used to evaluate shifts in the length frequency distributions of Potomac sculpin between the removal and reference subsections after 30 d. Results were considered significant if ($P < 0.05$).

Results

90-m Sampling

During the initial June 2005 sampling of the eight 90-m sampling areas, we collected and marked 3,353 Potomac sculpin. The capture efficiency of Potomac sculpin during the three-pass depletion population estimates averaged 65.1% (range = 52.5–77.4%) during the first pass. Population density of Potomac sculpin averaged 132 fish/100 m² (range = 30–297 fish/100 m²). We captured 16 species of fish in the study area. Potomac sculpin were the numerically dominant fish species and were followed in density (20–40/100 m²) by fantail darter *Etheostoma flabellare*, eastern blacknose dace *Rhinichthys atratulus*, and longnose dace *R. cataractae*. Lowest in density (<5/100 m²) were white sucker *Catostomus commersonii*, green sunfish *Lepomis cyanellus*, creek chub *Semotilus atromaculatus*, bluehead chub *Nocomis leptoccephalus*, common shiner *Luxilus cornutus*, bluntnose minnow *Pimephales notatus*, rock bass *Ambloplites rupestris*, yellow bullhead *Ameiurus natilis*, northern hog sucker *Hypentelium nigricans*, rainbow trout *Oncorhynchus mykiss*, and brook trout *Salvelinus fontinalis*.

Potomac sculpin recaptured 30 d later tended not to move: NM (80.4%), US (16.5%), DS (3.2%) (chi-square = 333.46; df = 2; $P < 0.001$). Recaptured Potomac sculpin that moved after 30 d preferred US (85%) to DS (15%) movement (chi-square = 35.39; df = 1; $P < 0.001$). Potomac sculpin recaptured 367 d later also showed a preference for not moving: NM

(62.5%), US (25.0%), DS (12.5%) (chi-square = 7.73; df = 2; $P < 0.021$). Potomac sculpin that moved after 363 d preferred US (66%) to DS (33%) movement, but the difference was not significant (chi-square = 0.88; df = 1; $P > 0.347$). The shift in the proportions of NM, US, and DS movers between 30 and 367 d was significantly different (Pearson's chi-square = 12.06; df = 2; $P = 0.0024$). The proportion of NM decreased by 18% while US (8%) and DS (10%) proportions increased. Total length did not affect movement of Potomac sculpin. There were no statistical differences (ANOVA: df = 3; $F = 0.514$; $P = 0.766$) in mean length among the recapture groups (NM, movers [US and DS movers combined], US movers, or DS movers).

Recolonization of removal subsections was rapid. Reference and removal subsections did not differ in the percentage change in population density 30 d later (*t*-test: $t = 12.1$; df = 1; $P > 0.45$). The summer drop in the hydrograph (wetted width was similar; average depth decreased) resulted in a decrease in population density for all sample areas. Removal sections averaged 56% (SD = 11.5) of previous population densities compared with a 58% (SD = 19.7) average in the reference sections. The mean lengths (*t*-tests: $P > 0.05$) and the length frequency distributions (Pearson's chi-square: $P > 0.05$) of Potomac sculpin did not change after 30 d in any of the removal ($n = 4$) or reference ($n = 4$) subsections.

The removal subsections influenced upstream movement but not downstream movement. There were statistical differences (Mann–Whitney *U*-test: $u = 16$; $P < 0.05$) between the rankings of the average percentage of Potomac sculpin that moved upstream and stayed in the removal subsections (9.5%; SD = 4.4%; range = 4.4–15.1%) and those that moved upstream and stayed in the reference subsections (2.6%; SD = 1.2%; range = 1.4–3.8%) (Figure 2). There were no statistical differences (Mann–Whitney

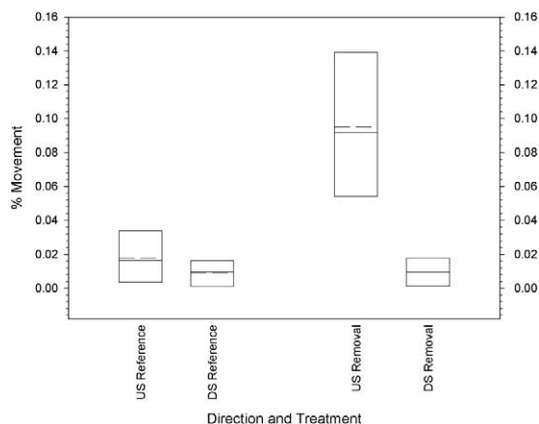


FIGURE 2.—Box plots of the percentage of upstream (US) and downstream (DS) movement into reference (B) and removal (B) subsections. Dashed line equals mean density; solid line equals median density. The box represents 50% of all values. $N = 4$ for all box plots.

U -test: $u = 6.5$; $P > 0.05$) between the rankings of the average percentage of Potomac sculpin that moved downstream and stayed in a removal subsection (0.8%; $SD = 0.87\%$; range = 0.0–1.9%) and those that moved downstream and stayed in a reference subsections (1.0%; $SD = 0.8\%$; range = 0.0–1.7%) (Figure 2).

Neither the total fish density nor the densities of Potomac sculpin were correlated with upstream movement. The total fish density in the immediate downstream subsection (C) was not correlated with upstream movement into the middle sections (B) after 30 d (Spearman's rank correlation coefficient: $r_s = -0.261$; $P > 0.05$). The density of Potomac sculpin in the immediate downstream subsection was not correlated with upstream movement into the middle sections after 30 d (Spearman's rank correlation coefficient: $r_s = 0.023$; $P > 0.05$).

3.14-km Sampling

During one-pass electrofishing through the 3.14-km sampling area in August 2005 (which included all eight 90-m sampling areas), we collected 7,610 Potomac sculpin. We recaptured 11.4% of the Potomac sculpin previously marked 75 d earlier in the 90-m sampling areas.

Marked Potomac sculpin recaptured 75 d later showed a preference for not moving: NM (64.5%), US (29.6%), DS (5.8%); (chi-square = 113.06; $df = 2$; $P < 0.001$). Potomac sculpin that moved after 75 d preferred US (84%) to DS (16%) movement (chi-square = 34.69; $df = 1$; $P < 0.001$). The distribution of the three groups was skewed (skewness = 8.48) and showed significant evidence of leptokurtosis (An-

scombe–Glynn kurtosis test: kurtosis = 91.66; $z = 12.82$; $P < 0.001$) (Figure 3). The average US movement was 104 m (maximum = 1,711 m). Of those US movers, 9.7% moved more than 250 m. The average DS movement was 65 m (maximum = 254 m).

During one-pass electrofishing sampling through the 3.14-km stream section in August 2006, we collected 6,684 Potomac sculpin. Marked Potomac sculpin recaptured 363 d later showed a preference for not moving: NM (53.4%), US (31.8%), DS (14.8%) (chi-square = 10.37; $df = 2$; $P < 0.006$). Potomac sculpin that moved after 75 d preferred US (68.3%) to DS (31.7%) movement, but the difference was not statistically significant (chi-square = 2.87; $df = 1$; $P > 0.090$). The distribution of the three groups was skewed (skewness = 4.49) and showed significant evidence of leptokurtosis (Anscombe–Glynn kurtosis test: kurtosis = 22.25; $z = 6.34$; $P < 0.001$) (Figure 3). The average US movement was 217 m (maximum = 1,255 m). Movement of greater than 250 m occurred in 21.4% of US movers. The average DS movement was 40 m (maximum = 127 m).

The proportions (NM, US, and DS) of recaptured Potomac sculpin changed between 75 and 363 d (Pearson's chi-square = 9.29; $df = 2$; $P = 0.0095$). The proportion of NM decreased by 12%, while US and DS proportions increased by 2% and 9%, respectively.

Stream Temperature and Flow

The water temperature conditions during all aspects of the study were suitable for sculpin (Jenkins and Burkhead 1993), and Potomac sculpin were commonly found throughout the entire 3.14-km study area. During the 30-d recolonization experiment (June 2005 to July 2005), there was no difference in the mean, maximum, or minimum water temperatures between the reference and removal treatment sections. The water temperature between the original marking (June 2005) and the first sampling of the entire 3.14-km study area 75 d later averaged 18.9°C. The range in water temperatures throughout the 367 d study ranged from 3.0°C to 24.2°C.

The calculated bank-full discharge at the hydrograph was 441 cubic feet per second (cfs). The median flow during the entire study period was 8.10 cfs. Flows exceeded 4.55 cfs 25% of the time. Between the 30 and 75 d time intervals of the first 90 m and 3.14-km samplings, the stream was at base flow conditions (<5.00 cfs) and no bank-full events were recorded. During the entire study there were two bank-full discharges with two large flood events (2,671 and 8,966 cfs) between the end of the first and beginning of the second 90-m and 3.14-km sampling periods.

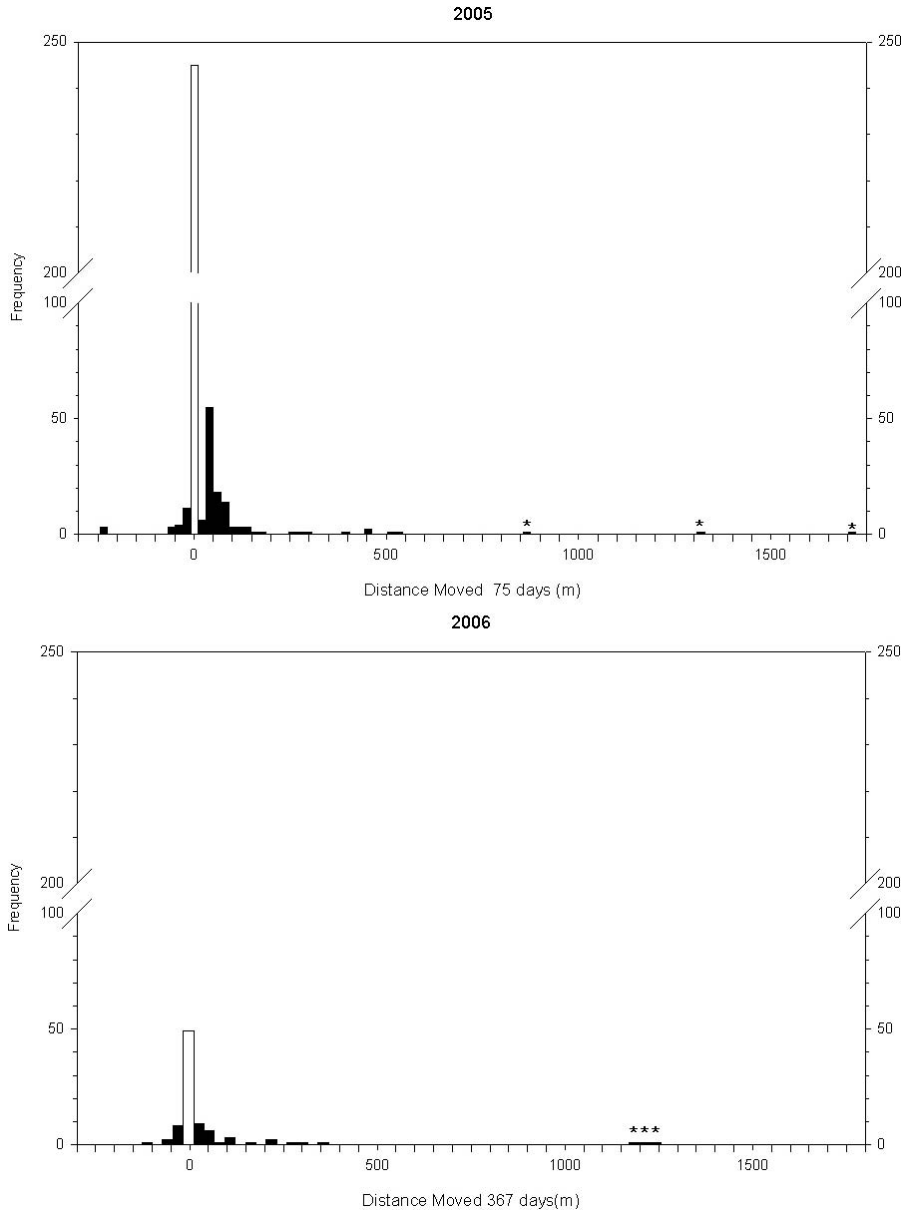


FIGURE 3.—Histogram of the movement of recaptured Potomac sculpin after 75 d ($n = 381$) and 367 d ($n = 81$) within the 3.17-km stream reach. Hollow bar represents Potomac sculpin recaptured within the original subsection where they were marked. Solid bars to the right of zero represent upstream movement and solid bars to the left of zero represent downstream movement. An asterisk (*) denotes less than five occurrences.

Discussion

Our results both mirror and differ from previous congeneric freshwater sculpin studies. As in other studies, we found that the majority of Potomac sculpin either did not move or did not move very far. Natsumeda (1999) hypothesized that many freshwater sculpins show residential tendencies during the non-

breeding season because of high fidelity to resting sites. However, the percentage of Potomac sculpin that moved in our study was much greater than in other studies and tended to increase over time (up to 1 year). Similar to the results of McCleave (1964), Potomac sculpin showed a preference for upstream movement, and this trend expanded with time. Similar to the

findings of Brown and Downhower (1982) and Schmetterling and Adams (2004) with freshwater sculpins, we found the length of Potomac sculpin did not affect movement. Several flood events occurred during our study, and we found, as did Anderson (1985), that floods did not increase movement rates. We hypothesized that the flood effect, if any, would increase downstream movement. However, most Potomac sculpin were nonmovers, and those that did move showed an upstream bias. This upstream bias is in contrast to several studies of freshwater sculpins that did not find a preference for upstream movement (Brown and Downhower 1982; Natsumeda 1999; Petty and Grossman 2004). However, the Brown and Downhower (1982) study design did not allow them to detect large movements upstream or downstream. We recaptured Potomac sculpin that exceeded maximum movement distances reported in the literature for cogenetic freshwater sculpins. Tagging a large number of fish and sampling over an extensive area allowed us to identify the small percentage of Potomac sculpin that moved great distances. After 75 d, 10% of the upstream movers moved more than 250 m (21% after 363 d). The maximum distance moved was 1,711 m in 75 d. Only Natsumeda (1999) and Schmetterling and Adams (2004) found movement over 200 m (290 m and 209 m, respectively). These long-distance movers can be a key to recolonization of habitats lost to stochastic or anthropogenic events. Recolonization by fishes thought to be sedentary may, in fact, occur relatively quickly because of these few long-distance movers.

Our removal sections were quickly recolonized, and we found that removal sections influence upstream, but not downstream, movement into or through these sections. These results are similar to those of Morgan and Ringler (1992), which found no significant differences in slimy sculpin densities among their treatments (removal sections, addition sections, and reference sections) after 98 d, potentially because of rapid movement into the sections by unmarked sculpin. The percentage moving into the removal sections (8.36%) was greater than the percentages for the reference (3.73%) or addition sections (1.44%).

Many factors can influence fish movement, and one must use caution in extrapolating results from this or other studies. Movements can be affected by the time of year, particularly during spawning periods. Natsumeda (1999) found slightly higher movements of the Japanese fluvial sculpin during breeding season. We believe that most of the movement during our study was not related to spawning, as we observed the peak of spawning activities to be from March 15 to April 15, and most of our sampling occurred in June, July, or August. Short-term recolonization and movement may

have been different if we sampled closer to spawning times. The lack of large potential predators of Potomac sculpin (i.e., salmonids, rock bass *Ambloplites rupestris*) in Smith Creek may also have affected behavior and movement needs at many scales. The density of Potomac sculpin in our study was considerably higher than would be predicted from other streams with similar widths (Anderson 1985). Anderson (1985) found a consistent relationship between freshwater sculpin density and stream width and hypothesized that a reduction in density with increasing stream width was related to the presence of predators (i.e., salmonids, rock bass) in wider streams.

Habitat quality may also affect movement. Smith Creek is generally devoid of riparian cover. Morgan and Ringler (1992) found that summer densities of slimy sculpin did not differ significantly between open- and closed-canopy habitat types. In contrast, Hawkins et al. (1983) found that freshwater sculpins were more abundant in streams without riparian shading because those streams had higher insect productivity.

Differences in movement found among the various freshwater sculpin studies could also be explained by the capture method used. Past studies have used either electrofishing or trapping to collect fish. Electrofishing is a more disruptive technique than individual net or trap capture and may have triggered or disrupted normal sculpin movement or behavior for a short time (<30 d). However, any shocking-induced movement should be limited to small distances because previous studies have found sculpin not moving out of very small home ranges (i.e., <20 m). Both study area and observed movement greatly exceeded that range. Because we wanted to mark large numbers of fish over a 3.14-km study area, conduct population estimates on all fishes, and evaluate movement for more than 30 d, we chose electrofishing as our capture method.

As with all mark-recapture studies, we do not know the fate of the marked fish that were never recaptured. In past freshwater sculpin studies, the percentage of recaptures usually dropped dramatically after 30–60 d (Bailey 1952; McCleave 1964; Brown and Downhower 1982; Warren and Pardew 1998; Natsumeda 1999; Schmetterling and Adams 2004). We tried to balance our sampling design to capture sufficient numbers of marked Potomac sculpin to test movement metrics over both short and long time spans, in addition to increasing the likelihood of capturing long-distance movers. A combination of intensive three-pass sampling on the 90-m sections and extensive one-pass sampling on the entire 3.14-km stream section met our criteria. Gowan et al. (1994) argued that movement rates for stream fishes are often underestimated because

of limitations of the study design. Specifically, Albanese et al. (2003) describes the effects of distance weighting on mark-recapture movement studies. We limited distance weighting in our design by (1) conducting uniform sampling of a large recapture zone, (2) having a high proportion of total possible movements sampled for each distance, and (3) sampling a reach with no tributaries (Albanese et al. 2003). We would have had higher recapture rates but lower or uneven detection of long-distance movers, if we did more intensive sampling nearer the original tagging locations or if we sampled within the first 30 d. Because our Potomac sculpin were not individually marked, some of the 1,174 recaptures may have been repeats (anywhere between one and four times). Based on the order of our sampling and the numbers recaptured, the cumulative total recapture of marked sculpin could be anywhere between 20% and 35%. This recapture percentage is within the range reported in the freshwater sculpin literature (Table 1), especially given the larger stream size and the time durations in this study. We believe both the recapture numbers and percentages are adequate for describing the movement metrics of this population. High recapture rates can be indicative of a population experiencing low rates of movement (Petty and Grossman 2004), or it can be indicative of frequent sampling of small streams a short time after marking.

Morgan and Ringler (1992) found slimy sculpin mortality to be 43% between June and September of their study period. Similar mortality rates over the course of this 367 d study could in part explain why many Potomac sculpin were never recaptured. We do not believe that sampling mortality, sampling bias, or mark retention or recognition was a reason why many fish were never recaptured. We came to this conclusion because (1) we observed very little sample mortality; (2) we sampled approximately twice the maximum movement distance; (3) tag recognition was excellent in the field; (4) tag retention, recognition, and survival ($n = 57$) was 100% for Potomac sculpin during a 60-d aquarium study; and (5) we have found marked sculpin more than 400 d after marking.

Debate exists on whether a tendency for movement is a fixed trait in a species. Petty and Grossman (2004) suggested that a potential reason for low movement rates among freshwater sculpin in North Carolina was their poor swimming ability and that they would have no need to move if refuge, food, and reproductive habitats were close by. In our study the reputed poor swimming ability of Potomac sculpin and the availability of suitable refuge and food habitats did not prevent some Potomac sculpin from moving great distances. As in Petty and Grossman (2004), leptokur-

tosis was a general feature of the sculpin movement distributions in our study. Leptokurtosis can be an indication of significant intrapopulation variability in movement rates (Skalski and Gilliam 2000; Petty and Grossman 2004). We do not know if the Potomac sculpin population in Smith Creek comprises both mobile and sedentary subpopulations or whether individuals switch between mobile and sedentary behavior. In either case, the ability to move long distances appears to be by "choice" and not because of poor swimming ability.

Petty and Grossman (2004) also suggested that the low mobility of mottled sculpin may be affected by high population density. Intraspecific interactions over habitat patches occupied by other sculpin may make it difficult for a sculpin to increase its fitness by moving once it occupies an acceptable habitat patch. In our study, population density was not correlated with movement into adjacent subsections. However, regardless of adjacent population densities, vacant habitat in the removal sections led to increased settlement (moved and stayed) of upstream movers but not to increased settlement of downstream movers. Occupied reference sections had very little upstream or downstream movement into them regardless of the population densities of adjacent subsections. Over the 3.14-km study area, the long-range movement of Potomac sculpin included movement through habitats that supported both high and low population densities of total fishes and Potomac sculpin.

Management Implications

Recolonization by sedentary fishes may be relatively quick because the average movement does not reflect population responses. A small percentage of movers in a large population may be all that is necessary to rapidly recolonize available habitat. Based on average density, one-pass electrofishing results, and average capture efficiency, our study stream reach has, by conservative estimates, more than 10,000 Potomac sculpin. Even if only a small percentage of these sculpin are mobile, those fish could easily explain the rapid recolonization rates in our removal subsections. The long upstream movement found in our study is much greater than previously reported for any species of freshwater sculpin and could provide possible insight into successful recolonization of habitats where there is no upstream source population. These long-distance moving fishes can be a key to recolonization of habitats lost to stochastic events or anthropogenic activities.

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